BOOK REVIEW

Campos-Ortega, J. A. and V. Hartenstein. 1985. The Embryonic Development of *Drosophila melanogaster*. Springer-Verlag. Berlin, Heidelberg, New York,Tokyo. 227 pp., 85 figs., 2 tables, subject index. $120.00Can.

Flies of the species *Drosophila melanogaster* are arguably the best understood of all higher animals because of their enormous popularity with geneticists since 1909 when T. H. Morgan first started culturing them in his "fly room" at Columbia University. To-day they are the organisms of choice for legions of highly ingenious and pecunious developmental biologists interested in understanding how genes control cell determination and differentiation in higher animals.

In the last decade, a flood of papers have appeared on the genetic basis of cell determination and pattern formation in *Drosophila* embryos--most recently on the mode-of-action of genes controlling segmentation of the germ band (segmentaion genes) and longitudinal specification of segment identity (homoeotic genes). Most of these papers have been based on use of genetic dissection methods and have involved analysis of mutant embryonic and larval phenotypes (more recently, use of recombinant DNA and immunocytochemical techniques has predominated). However, in spite of this explosion in experimental results, the standard description of normal embryogenesis against which they are compared has remained Sonnenblick's and Poulson's superb but now out-of-date chapters in Demerec's (1950) *Biology of Drosophila* (updated but with little added by Fullilove and Jacobson [1978] and Bownes [1982]). Campos-Ortega and Hartenstein's new book supplants these classic accounts with style and depth (it is dedicated to Donald F. Poulson).

Eggs of *D. melanogaster* average 0.42 x 0.15 mm and require about one day to develop from fertilization to hatching at 25°C. This development is described in great detail in the eight chapters of this book. Chapter 1 (6 pp.) presents a brief, illustrated (12 drawings), summary of embryogenesis in this species and chapter 2 (75 pp.) a system for staging it. The authors divide embryogenesis into 17 stages ranging in length from 10 min (each of stages 6 and 7) to 11.7 hr (stage 17) and summarize the events occurring in each stage. These events are illustrated with 71 photomicrographs of living whole mounts and 123 of fixed embryos embedded in plastic and sectioned longitudinally or horizontally.

Origin and differentiation of most organ systems are considered in Chapter 3 (79 pp.) – including the gut, Malpighian tubules, salivary glands, gonads, somatic and visceral musculature, dorsal vessel, fat body, epidermis, central (CNS), peripheral (PNS) and stomatogastric (SNS) nervous systems and the tracheal system. The chapter is illustrated with 42 drawings, 56 photomicrographs and seven transmission electron micrographs – the most impressive of the drawings being Fig. 3.14 (a lateral view of a first instar larva with every external cuticular structure illustrated), Figs. 3.23-3.25 (detailed, 3-dimensional reconstructions of all external sensilla and their projections to specific ganglia of the CNS in both ventral and lateral aspect), and Fig. 3.30 (six 3-dimensional reconstructions illustrating neurogenesis of the CNS). (The origin and differentiation of the CNS is remarkably similar to that recently described in great detail in various grasshopper embryos by Goodman, Bate and their colleagues).

The pattern of embryonic cell division is summarized in Chapter 4 (7 pp., 6 drawings) and is shown to occur during two periods. The first takes place prior to cell formation at blastoderm and involves 13 rounds of mitosis. The first seven zygotic divisions are synchronous and yield a

syncytium of 128 nuclei distributed as an ellipsoid within the yolk. With the next 3 mitoses (8-10), the resulting nuclei approach the peripheral periplasm to form the syncytial blastoderm with 200 nuclei remaining behind in the yolk as vitellophags and 17-18 entering the posterior pole plasm to form pole cells (germ line cells). Three further (11-13) and now parasynchronous mitoses increase the number of syncytial blastoderm nuclei to about 5000 at which time cell membranes form between adjacent nuclei. During the second period of mitosis, from blastoderm formation to hatching, most cells divide only two or three more times - exceptions being the teloblastic nerve mother cells (neuroblasts) of the CNS, sensillar stem cells and pole cells.

Chapter 5 (13 pp., 16 drawings) considers the morphogenetic movements involved in changing the simple cellular monolayer of the blastoderm into the complex, 3-dimensional structure of the young embryo. These movements occur either by growth and infolding of certain regions of the blastoderm or by movement of cells or groups of cells into the interior and can involve cell proliferation, changes in cell shape and size, and shifting of individual cells in relation to each other. Gastrulation, germ band elongation and (later) shortening, head involution and dorsal closure are among the more important of these movements in *Drosophila* embryogenesis. With gastrulation, 1250 cells invaginate from the ventral midline of the embryo to form mesoderm and endoderm leaving 3750 cells about the yolk to form the rest of the larval body (ectoderm). The germ band elongates 220% around the posterior end of the egg during germ ban elongation and later, during its shortening, each thoracic and abdominal segment shortens and broadens – a shape change attained through shape changes of their individual cells.

Cephalogenesis (Chapter 6-13 pp., 9 drawings, 11 photomicrographs) includes head involution, a phenomenon unique to higher Diptera (Cyclorrhapha). At stage 11, the developing head is similar to, though less complex than, heads of other insect embryos at comparable stages of development and contains a large procephalon and three gnathal segments each bearing a pair of short, blunt, appendages. Portions of all these segments shift cephalad during the remainder of embryogenesis and invaginate into the front of the embryo to form the atrium of the foregut in which is later secreted the cuticle of the larval cephalopharyngeal skeleton. The segmental source of the various parts of this skeleton are indicated (the mouth hooks, for example, derive from the maxillary appendages).

Certain aspects of segmentation are considered in more detail in Chapter 7 (12 pp., 8 drawings, 2 tables) including formation of segmental borders, epidermal sensory organs, muscle innervation, and homologies between the muscles and sense organs of each segment.

The final chapter (8- 8 pp., 2 drawings) presents a new fate map of the *Drosophila* blastoderm. This was derived by use of three methods: 1. The enzyme horse radish peroxidase (HRP) was injected into donor eggs before cellularization. This tracer spreads freely throughout each embryo and becomes incorporated into all its cells during cellularization. Just after cellularization, labelled cells are taken from these donors by means of a micropipette and transplanted singly into unlabelled host embryos. The progeny of each transplanted cell is then traced during subsequent development of the host embryo. 2. Progressively older embryos were removed from their choria and vitelline membranes and stained with fuchsin (every nucleus can be counted and drawn in such embryos) 3. Planimetric reconstructions of complete series of sections of embryos of similar age were prepared by "rolling off" folded and invaginated tissues. Use of these methods enabled the authors to obtain reliable quantitative data for each embryonic stage. Fig. 1B illustrates this fate map for one side of the blastoderm and indicates

the number of blastoderm cells contributing to each larval organ derived from that side (for example, 150 blastoderm cells give rise to one half the proctodeum). The rest of this chapter considers cell number in each organ and the number of blastoderm cells giving rise to it.

Production quality of the book is outstanding, for paper, printing and binding, and the halftones of the photomicrographs are of uniformly high standard. This last was because all sections were cut from eggs dechorionated and fixed according to Zalokar and Erk's (1977) phase-partition method (which causes essentially no disruption of egg contents) and embedded in plastic. There are a few typographical errors and some awkward grammar but not much, considering that the senior author is Spanish and the junior author German. My principal criticisms are its outrageous price, the total absence of scanning electron micrographs (available from the work of Turner and Mahowald [1976–1979] and cited in the book), and the almost total absence of reference to embryos of other insects (only Goodman *et al*'s work on grasshopper neurogenesis, Anderson's (1962, 1972) synopses, and Wheeler's (1891, 1983) and Weisman's (1863) classical descriptive studies are mentioned). Their discussion of head segmentation in chapter 6, for example, would have been vastly improved had they referred to Rempel's (1975 Quaest. Ent. 11: 7-25) critical review of this topic. (This subject has recently been considered at great length for this species by Jürgens *et al.*, Rous's Archives of Developmental Biology 195: 359–377. [1986]). There are only 112 references.

However, this book was written for *Drosophila* workers--not for comparative embryologists or entomologists--and as such will be indispensible to all individuals investigating the embryos of these insects (most recent papers cite it). There are no descriptive studies of the embryos of other insects that even approach this study in detail, and it is now the standard of excellence against which all future such investigations will be compared.

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